Animal Behaviour 90 (2014) 31–39

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Phenotypic plasticity in nest departure calls: weighing costs and benefits

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ARTICLE INFO

Article history:
Received 19 September 2013
Initial acceptance 26 November 2013
Final acceptance 3 January 2014
Published online
MS. number: A13-00781R

Keywords:
behavioural plasticity
communication
cost–benefit analysis
Melospiza melodia
nest departure call
nest guarding
song sparrow

In birds, male song has been extensively studied, but female vocalizations have received little attention. Females of several North American species produce a unique vocalization, the nest departure call (NDC), upon leaving nests. Producing NDCs has costs due to acoustical properties that make nests easy to locate by predators. Thus, NDCs must also have benefits that balance or outweigh costs, and females should modulate call production as costs and benefits change. We explored whether female song sparrows, *Melospiza melodia*, adjust calling rate to reflect differential costs and benefits of calling induced by male presence, male quality (measured by body mass and song complexity), nest predator presence and nest height. Results suggest that calls benefit females by promoting male nest guarding and that females display adaptive plasticity in call production. Specifically, calling rate increased when the male was present, and male nest guarding increased when females gave an NDC. Females called less in the presence of a model nest predator, probably because the perceived costs of predator attraction outweighed the benefits of male recruitment. Conversely, females with heavier mates called more, perhaps because the efficacy of male nest guarding increases with mass. In addition, females called more from elevated nests in the presence of the predator and decreased calling later in the day. Male song complexity failed to predict calling rate, suggesting that this sexually selected trait does not reflect direct benefits gained by producing an NDC. Plasticity in calling probably exists because context-appropriate communication elevates fitness, whereas contextual mistakes in the decision to communicate result in fitness declines.

The complex and prominent vocalizations of male songbirds are the focus of extensive study (Nowicki & Searcy, 2004; Searcy & Andersson, 1986). However, the subtler vocalizations of females have received little attention (Gorissen & Eens, 2005; McDonald & Greenberg, 1991). One unique type of female vocalization that has been recorded in at least 15 species of North American passerines is the nest departure call (NDC). NDCs are initiated upon leaving the nest and have a characteristic acoustical structure (broadband frequency, short note duration and repetitiveness) that makes nests easy to localize and also acts to project flight trajectory (McDonald & Greenberg, 1991; Fig. 1).

Passerine nests are vulnerable to predation, and nest depredation has played a pivotal role in driving the evolution of species-level differences in incubation behaviour (Conway & Martin, 2000; Martin, 1995; Martin, Scott, & Menge, 2000; Ricklefs, 1969). Thus, the adaptive function of highly conspicuous calls, given from nests and open to exploitation by predators, evades easy explanation. Indeed, empirical research has demonstrated that giving NDCs can increase nest predation rates (McDonald & Greenberg, 1991; Yasukawa, 1989) as well as parasitism by brown-headed cowbirds, *Molothrus ater* (Clotfelter, 1998). Thus, NDCs must have benefits that override these costs. Previously hypothesized benefits of calling include recruiting male vigilance for nest guarding during female absence (McDonald & Greenberg, 1991; Yasukawa, 1989), decreasing harassment of females by males that may mistake them for territorial intruders (Beletsky & Orians, 1985; Edwards, 1987; McDonald & Greenberg, 1991), advertising female receptivity, discouraging settlement of other females on the territory, distracting predators (McDonald & Greenberg, 1991) and recruiting males to mate-guard during incubation off-bouts (Fedy & Martin, 2009; McDonald & Greenberg, 1991).

However, due to the paucity of work on this behaviour, the actual functions of these calls and the associated costs and benefits remain poorly understood (McDonald & Greenberg, 1991). Moreover, communication systems have evolved to elevate fitness, but signalling in the wrong context may result in fitness declines (Zuk &

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0003-3472/$38.00
http://dx.doi.org/10.1016/j.anbehav.2014.01.010

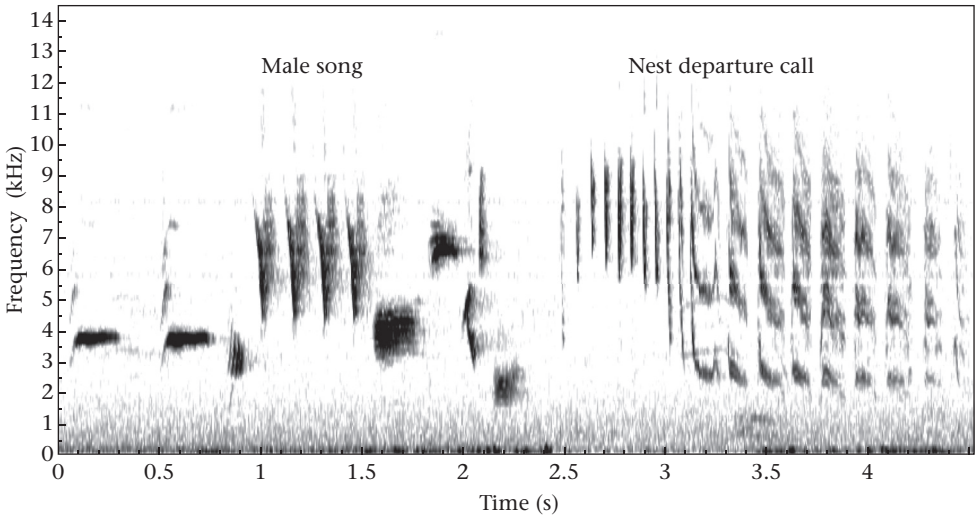

Figure 1. Nest departure call of a female song sparrow, shortly following a male song. Note the characteristic broadband frequency, short note duration and repetitiveness of the call. Nest departure calls and nest departures are often associated with the male singing in close proximity to the nest.

Kolluru, 1998; Zuk, Simmons, & Rotenberry, 1995). Thus, individuals should exhibit phenotypic plasticity in calling behaviour (Lima & Dill, 1990; McNamara & Houston, 1996; Stearns, 1989). However, no study has comprehensively investigated whether females adjust calling behaviour in a context-dependent fashion to maximize benefits and minimize costs. We address these gaps in understanding by addressing novel questions about the function and context dependency of NDCs in female song sparrows, *Melospiza melodia*. Our study had five primary objectives, which we outline below.

First, we explored whether females plastically adjust NDC production in a fashion consistent with the hypothesis that these calls function as a signal to increase male vigilance during incubation off-bouts. Given a male recruitment function, benefits of calling should be high when the male is near and available to nest-guard, but calling should have little adaptive benefit in absence of the male, such that calling rate increases in the presence of the male. The benefit of calling should also be manifest by an increase in male nest-guarding behaviour during incubation off-bouts following an NDC. Although the efficacy of nest guarding is unclear in the song sparrow, the behaviour is well documented (Hatch, 1997; Weatherhead, 1989), and as pointed out by Hatch (1997), it is unclear why the behaviour would persist if it has no potential to deter predators.

Second, we sought to determine whether the presence of a nest predator affects female call production. Avian nest predators have highly developed auditory systems and may thus use NDCs to locate nests (Eggers, Griesser, Nystrand, & Ekman, 2006; Martin, 1987a; Peluc, Sillett, Rotenberry, & Ghalambor, 2008). Thus, we predicted that females would reduce call production in the presence of perceived corvid nest predation risk as an adaptive means of reducing the likelihood of nest predation.

Third, we examined whether male quality modifies female calling behaviour. Specifically, we considered effects of two indicators of male quality on NDC production: body mass and song complexity. More massive males may be larger or may be in better body condition and have higher energy reserves. Thus, heavier males may be more effective at nest defence either due to larger size, or because they need to devote less time to foraging and self-maintenance (Martin & Horn, 1993; Sproat & Ritchison, 1993; Wallin, 1987; Winkler, 1992). In addition, greater mass may reflect high territory quality, which may increase both foraging efficiency and time available for vigilance (van de Crommenaker, Komdeur, Burke, & Richardson, 2011; Drent & Daan, 1980; Komdeur, 1992; Martin, 1987b; Svensson & Nilsson, 1995). Thus, we predicted that benefits of calling and NDC production increase with male body mass. Song complexity is the basis for female choice in many species, including *M. melodia* (Nolan & Hill, 2004; Nowicki & Searcy, 2004; Searcy, 1984; Searcy & Andersson, 1986; Searcy & Yasukawa, 1996), and female choice of males with complex songs may be motivated by direct benefits gained in the form of paternal assistance. Thus, we predicted that benefits of calling and NDC production would increase with male song complexity (Buchanan & Catchpole, 2000; Hill, 1991; Hoelzer, 1989). However, an alternative hypothesis is that females choose males with complex songs primarily for indirect benefits, and males with more complex songs trade off mating effort against paternal effort (Burley, 1988; Møller & Thornhill, 1998; Qvarnström, Pärt, & Sheldon, 2000). In this case, nest-guarding services and NDC production might decline with song complexity. Furthermore, with respective to male quality in general, we predicted that female call production would decline less in the presence of the predator when the male was of higher quality, since benefits of male recruitment and guarding might offset costs of predator attraction in this case.

Fourth, we explored the effect of nest site location on calling behaviour (Eggers et al., 2006; Martin, 1987a; Martin, 1995; Martin et al., 2000; Peluc et al., 2008). More concealed nests may be more difficult to locate, lowering costs of calling. Indeed, across avian taxa, NDCs are given almost exclusively by species occupying marshland or grassland habitat, where dense cover may provide a buffer against nest detection (McDonald & Greenberg, 1991). Furthermore, among open-cup passerines, ground nests are subject to the lowest predation rates, with nests elevated in the canopy or shrubs experiencing higher depredation (Martin, 1993, 1995; Peluc et al., 2008). In song sparrows at our study site, nests on the ground tend to be more concealed than elevated nests (M. L. Grunst, A. S. Grunst, & J. T. Rotenberry, personal observations). Moreover, elevated nests are more exposed to attack from above by visually oriented corvid predators (Martin, 1987a; Peluc et al., 2008). Thus, we predicted that costs of calling at elevated nests would outweigh benefits, resulting in higher calling rates at ground nests than at elevated nests, and that this effect would be magnified in the presence of the predator.

Finally, our fifth objective was to establish whether NDC production covaries with other aspects of incubation behaviour. Specifically, we were interested in whether recruitment of the male via NDCs allows females to spend more time off the nest engaging in self-maintenance activities, such that off-bout length increases and overall nest attentiveness decreases as a function of giving the call. By establishing whether male–female communication via the NDC affects optimal patterns of incubation, we hoped to gain insight into the underexplored contingency that interactions between mated partners modify patterns of parental effort in biparental species (Fedy & Martin, 2009).

METHODS

Study Species and Site

We studied NDCs in song sparrows breeding near the University of California's Sierra Nevada Aquatic Research Laboratory (SNARL) on the eastern slope of the Sierra Nevada (Mono County, CA, U.S.A., 37°36′51″N, 118°49′47″W). Focal pairs occupied territories along the riparian corridors of Convict Creek and McGee Creek. Convict Creek flows through SNARL. McGee Creek is located about 16 km south of SNARL in the Inyo National Forest (37°33′20″N, 118°47′35″W). Both sites are at mid-elevation (2100–2500 m). Interestingly, McDonald and Greenberg (1991) reported that *M. melodia* females generally do not produce NDCs. However, females from Mandarte Island and around Puget Sound do produce these calls (McDonald & Greenberg, 1991), as do females in our study population.

In *M. melodia*, the female alone incubates, whereas both females and males provision nestlings. However, males may contribute to parental care during incubation via nest guarding. Nest guarding may have a particularly potent impact on fitness during incubation off-bouts, when the female leaves the nest to forage and engage in other self-maintenance activities. In our song sparrow population, the mean ± SE incubation on-bout is 19.96 ± 1.08 min (range 7.39–48.44 min), and the mean off-bout length is 7.68 ± 0.49 min (range 2.02–24.25 min) (Grunst, Grunst, & Rotenberry, n.d.-a, n.d.-b). Male singing activity often increases near the nest during incubation off-bouts of females (M. L. Grunst, A. S. Grunst, & J. T. Rotenberry, personal observations).

High nest predation rates in our population (68.13%; Grunst et al., n.d.-a, n.d.-b) may increase the selective importance of NDCs and male nest guarding. We confirmed the identity of few predators. However, long-tailed weasels, *Mustela erminea*, and garter snakes (*Thamnophis* sp.) were seen removing nestlings. Furthermore, nests also faced high parasitism by brown-headed cowbirds, *Molothrus ater* (28.9%). Corvids, including western scrub-jays, *Aphelocoma californica*, Stellar's jays, *Cyanocitta stelleri*, and black-billed magpies, *Pica hudsonia*, and small mammals, including least chipmunk, *Neotamias minimus*, and deer mice, *Peromyscus maniculatus*, also contribute to predation on open-cup passerine nests in eastern Sierra riparian corridors (Latif, Heath, & Ballard, 2012).

Research Approach

Beginning in early May 2010–2012 we located and target-netted breeding pairs of *M. melodia* as part of a larger study on nesting behaviour. We used conspecific playback to lure males into mist nets (all males in our data set except one were banded), but we captured most females, and a few males, at nests. Because of the greater difficulty in capturing females, 14 females included in our data set were unbanded. However, unbanded females were easily identified based on their vicinity to an active nest. We uniquely banded birds with U.S. Geological Survey bands and an additional combination of three coloured leg bands. The breeding season extended through mid-August.

Field techniques were authorized by a U.S. Geological Survey bird banding permit (23035-F), a California state collecting permit (SC-11059), a federal migratory bird collecting permit (MB22670A-0) and a special use permit from the Inyo National Forest (MLD100008P). The Institutional Animal Care and Use Committee of the University of California (protocol A-20100002E) approved all animal use procedures.

Behavioural Observation and Predator Presentation Experiment

We located nests using a combination of systematic search and behavioural observation (Martin & Geupel, 1993). Once nests were located, we checked contents every 2–3 days to document nesting status. On days 2–8 of the incubation period, or as soon as the nest was located, we videorecorded nests using Canon 800 series camcorders under three experimental conditions: baseline, elevated perceived nest predation risk and negative control. We elevated perceived nest predation risk using a decoy and a recording of a western scrub-jay (Peluc et al., 2008). We also initially included a negative control treatment, consisting of a house finch, *Haemorhous mexicanus*. However, finch treatments were recoded as baseline for use in the final analyses (see below for justification). We placed decoys 6–10 m from nests and 2 m off the ground, and projected recordings of vocalizations using a MP3 player placed on the ground below decoys. We concealed camcorders 3–6 m from nests to prevent disturbance originating from the recording alone. Presentations were initiated between 0600 and 1400 hours Pacific Daylight Time (PDT). We controlled for time of day and date in statistical analyses. We performed all treatments on each nest sequentially, on the same day, in randomly assigned order. Time between treatments averaged 10 min, and each treatment lasted approximately 2 h. Presentation order had no significant effect on NDC production by females (generalized linear mixed effects model, GLMM: $Z = -0.59$, $\beta = -0.43 \pm 0.73$, $N = 409$ observations, 57 nests, 43 females, 41 males, $P = 0.55$) or guarding behaviour of males (GLMM: $Z = -0.08$, $\beta = -0.05 \pm 0.56$, $N = 409$ observations, 57 nests, 43 females, 41 males, $P = 0.93$). Models testing for an effect of presentation order on NDC production and guarding behaviour included the strong effects of male presence and NDC production, respectively (see Results). We measured nest height after the nest failed or the nestlings fledged.

Data Extraction from Video Recordings

We extracted NDC behaviour for each off-bout that occurred within the 2 h treatment period. Behaviour was extracted for a random subset of nests recorded as part of a larger study on effects of perceived predation risk on song sparrow incubation behaviour. We previously established that female song sparrows respond to scrub-jays as predators by reducing incubation attentiveness (percentage of time spent incubating eggs) relative to that under baseline conditions, but they do not alter incubation attentiveness in response to the house finch (Grunst et al., n.d.-a, n.d.-b; see Supplementary material, Table S1). Thus, we extracted data only on NDC behaviour from 10 finch recordings (the process is time intensive) and coded finch treatments as baseline for use in this analysis. Preliminary analysis indicated that females did not reduce calling behaviour in response to the finch, as would be expected if the finch was perceived as a disturbance or if the noise of the recording alone interfered with communication (GLMM: $Z = 1.45$, $\beta = 1.13 \pm 0.78$, $P = 0.14$). We analysed NDC behaviour from a sample including 427 nest departures, 61 nests, 41 males and 43

females. We extracted NDC data for both the predator and baseline treatments for 39 nests (336 nest departures, 30 males, 32 females), for the baseline treatment alone for eight nests (33 nest departures, 8 males, 8 females) and for the predator treatment alone for 14 nests (58 nest departures, 16 males, 13 females). Results were qualitatively the same when restricting the data set to the subset of nests for which we conducted both baseline and predator trials. The sample size for the final model predicting NDC production is reduced since we only measured the body mass of 35 males. The model used to test for covariation between NDC production and off-bout length excluded 32 nest departures for which the off-bout length was unknown because the recording ended before the female returned. In addition, we only measured the repertoire size of 36 males and the syllable diversity of 35 males. However, this change in sample size only affected the initial model predicting NDC production, male nest-guarding behaviour, and female incubation attentiveness/off-bout length, because song complexity traits were eliminated from final models due to nonsignificance.

We viewed recordings to determine when females departed the nest and whether an NDC was given upon each departure. Additionally, to determine whether the male was present before female departure from the nest, we recorded whether the male produced a song during the 3 min immediately prior to departure. If a song was produced during this period, then the male was considered present. The male was also occasionally seen during this period, but in all such cases, he also produced a song. If a song was not produced during this period, the male was considered absent (coded 1, 0). As a metric of male nest guarding we recorded whether the male produced a song in the 3 min following female nest departure. If the male produced a song, or was seen, during this period, he was considered present; if not, he was considered absent (coded 1, 0). This procedure for determining male presence could be prone to producing false negatives, since males might be present, but not vocal. False negatives could reduce our ability to detect a correlation between male presence and female calls, but should not otherwise affect the validity of statistical tests. Moreover, since male song may serve as a signal to females that the male is present and available to nest-guard, establishing a link between male song and the production of NDCs is pertinent in itself.

Measuring Body Mass and Song Complexity

Upon capture of males, we measured body mass (±0.1 g) using a digital scale, unflattened wing chord (±1 cm) using a wing scale and tarsus length (±0.01 cm) using digital calipers. We used body mass alone as a combined metric of male size and energy reserves, because the linear correlation between body mass and tarsus length was low and was not substantially improved by attempting to model nonlinearity into the relationship between mass and tarsus length (as suggested for the scaled mass index; Peig & Green 2009, 2010).

To obtain song of focal males, we used iMovie and Quicktime to extract .wav audio files from mini DVD tapes containing video recordings of incubation behaviour. We visualized 300 consecutive songs or 450 total songs per male using Raven Pro (Cornell Lab of Ornithology, Ithaca, NY, U.S.A.) (MacDougall-Shackleton et al., 2009; Pfaff, Zanette, MacDougall-Shackleton, & MacDougall-Shackleton, 2007). We measured two metrics of male song complexity: song repertoire size and song syllable diversity. We determined distinct song types upon song type switching in strings of vocalizations. Once repertoire size was established, we determined the total number of syllables within each male's repertoire by identifying unique syllables across song types (MacDougall-Shackleton et al., 2009).

Statistical Analysis

We used R 2.15.2 to conduct all statistical analyses (R Development Core Team, 2012). To assess effects of male presence, predation risk, male quality and nest height on the decision to produce an NDC, we used a generalized linear mixed effects model (GLMM, binomial family) implemented by the lme4 package in R (Bates, Maechler, & Bolker, 2012). The dependent variable was whether or not the female produced a call upon leaving the nest (coded 1, 0). We included treatment (baseline, predator), male presence (coded 1, 0), body mass, repertoire size, syllable diversity and nest site elevation (0 = on ground, 1 = off ground) in the model as fixed effects. We initially allowed for two-way interactions between treatments and all other independent variables, since we were interested in how costs associated with predator presence would modify relationships. We also included time and date in the model as covariates. When including date in statistical models, 1 May was coded as day 1. We entered nest number and male and female identity as random effects.

Second, to assess the effect of NDC production, predator presence and male phenotype on male recruitment to guard the nest, we again used a GLMM binomial model with guarding (coded 1, 0) as the dependent variable. We included treatment, NDC (coded 1, 0), body mass, repertoire size, syllable diversity and nest site elevation in the model as fixed effects and used the same interaction and random terms as described above.

Third, to test for covariation between NDCs and incubation behaviour, we used a linear mixed effects model (LMM; also implemented by the lme4 package in R) fitted using reduced maximum likelihood, with the length of the off-bout immediately following each nest departure entered as the dependent variable. We entered treatment, NDC (coded 1, 0), male body mass, repertoire size, syllable diversity and nest site elevation as fixed effects, and included the same interaction terms, random terms and covariates as described above. We transformed off-bout length by taking the cube root. We then used a linear mixed effects model to examine whether overall nest attentiveness (percentage of time incubating eggs) was influenced by the percentage of time that the female gave an NDC, predator presence, male characteristics and nest height. We squared incubation attentiveness to achieve normality. We did not use interaction terms in this model, but again included the same random terms and covariates described above. We also reran the above models using male guarding behaviour instead of NDC production as a predictor variable. We employed a Satterthwaite approximation (implemented by the lmerTest package of R; Kuznetsova, Brockhoff, & Christensen, 2013) for estimating degrees of freedom in LMM models. We sequentially reduced all models until remaining predictors were significant ($\alpha = 0.05$).

RESULTS

Characterization of NDCs and Male Guarding Behaviour

Song sparrow NDCs displayed the broadband frequency, short note duration and repetitiveness characteristic of NDCs described previously (Fig. 1). Females produced calls upon initiation of departure from the nest, often shortly after the male sang close by (Fig. 1). Overall, females produced NDCs at 33.72% of nest departures during incubation. The majority of females (66%, 28/42 individuals) displayed variation in NDC behaviour, producing an NDC upon some nest departures but not others. However, a few females never (21%, 9/42 individuals) or always (12%, 5/42 individuals) produced an NDC when leaving the nest.

Overall, males were present and singing near the nest, and thus determined to be guarding, following 65.33% of nest departures.

The majority of males (68%, 28/41 individuals) displayed variation in guarding behaviour, being present and singing near the nest following some female departures but not others. However, a few males never (10%, 4/41 individuals) or always guarded (22%, 9/41 individuals).

Variation in Predictor Variables

Song repertoire size of males ranged from 5 to 12 song types (mean ± SD = 8.85 ± 1.62 song types). Syllable diversity ranged from 25 to 43 syllable types (mean ± SD = 33.68 ± 4.49 syllable types). Body mass of males ranged from 18.4 to 22.2 g (mean ± SD = 20.5 ± 0.91 g). Although repertoire size and syllable diversity were positively correlated (Spearman rank correlation: $r_S = 0.55$, $N = 28$, $P = 0.56$), neither variable was correlated with body mass (repertoire size: $r_S = -0.26$, $N = 28$, $P = 0.17$; syllable diversity: $r_S = -0.12$, $N = 28$, $P = 0.56$). Nest height ranged from 0 to 1.96 m (mean ± SD = 0.24 ± 0.23 m). Of the 61 nests monitored, 43 (70%) were elevated in shrubs and 18 (30%) were located on the ground. Time of recordings ranged from 0539 to 1512 hours Pacific Standard Time (mean ± SD = 1003 hours ± 2.12 h). Date of recording ranged from 22 May to 30 July (mean ± SD = 28 June ± 18 days).

Nest Departure Call Production

Male presence, as indicated primarily through the production of song prior to nest departure, was the strongest predictor of females' decision to produce an NDC (Table 1). Females produced calls during a significantly greater percentage of nest departures when the male was present than when the male was absent (Fig. 2a). In addition, females produced fewer NDCs in the presence of the scrub-jay nest predator (Table 1, Fig. 2b). Females called more when their mate was more massive, and they called less frequently later in the day (Table 1). Finally, there was a positive interaction between nest site elevation and treatment, which reflected the fact that females produced the call more often in the presence of the predator when departing from elevated nests (Table 1). No other interactions were significant (GLMM: $P > 0.1$ in all cases; Supplementary Table S2) and female calling did not differ as a function of male repertoire size or syllable diversity (GLMM: $P > 0.1$; Supplementary Table S2).

Male Nest Guarding

Following female nest departure, males were significantly more likely to guard the nest, as measured by the production of nearby song, after an NDC was given than if the female produced no call (GLMM: $Z = 3.23$, $N = 427$ nest departures, 61 nests, 43 females, 41 males, $\beta = 1.18 \pm 0.37$, $P = 0.001$; Fig. 2c). This pattern did not depend on the presence of the nest predator, as there was no main effect of predator presence and no interaction between NDCs and the presence of a predator ($P > 0.10$ in all cases; Supplementary Table S3). Male body mass, song complexity and nest site elevation also failed to predict guarding behaviour, and there was no indication of additional interactions ($P > 0.10$ in all cases; Supplementary Table S3). Model results were qualitatively the same when we restricted the analysis to observations in which the male was present before nest departure.

Table 1
Generalized linear mixed effects model (binomial family) predicting nest departure call production by female song sparrows

	Estimate (β±SE)	Z	$P(>\|Z\|)$
Intercept	−23.63±9.89	−2.39	0.02
Male present	2.36±0.51	4.66	<0.001
Treatment	−2.12±0.88*	−2.42	0.01
Male body mass	1.19±0.48	2.50	0.01
Nest elevation	0.35±0.99	0.35	0.72
Time of day	−0.36±0.13	−2.82	0.005
Treatment×nest elevation	2.14±0.99	2.14	0.03

$N = 358$ nest departures, 52 nests, 42 females and 35 males.
* Predator (jay) treatment relative to baseline.

Covariation with Incubation Behaviour

Off-bout length was not significantly related to whether or not a female produced an NDC, although in the initial full model there was a trend towards a positive correlation between off-bout length and whether an NDC was produced (LMM: $P = 0.07$; Supplementary Table S4). Rather, off-bout length was positively predicted by an interaction between treatment and male mass (LMM: $F_{1,302} = 4.61$, $N = 329$ observations, 52 nests, 42 females, 35 males, $\beta = 0.13 \pm 0.06$, $P = 0.03$), reflecting the fact that females took longer off-bouts during the predator treatment if their mate was heavier. In addition, females with elevated nests took longer off-bouts (LMM: $F_{1,32} = 4.61$, $\beta = 0.17 \pm 0.08$, $P = 0.05$). In the model predicting off-bout length, the main effects of predator presence and male body mass were not significant (LMM: $F_{1,293} = 2.92$, $\beta = -0.09 \pm 0.06$, $P = 0.09$; LMM: $F_{1,47} = 1.01$, $\beta = -0.02 \pm 0.05$, $P = 0.31$, respectively). Total nest attentiveness (percentage of time spent incubating eggs) was unrelated to the percentage of time that a female gave a departure call, or to any other variable (LMM: $P > 0.10$, $N = 84$ observations, 45 nests, 35 females, 31 males; Supplementary Table S5). When included in models predicting female incubation behaviours instead of NDC production, male guarding was unrelated to both off-bout length (LMM: $F_{1,238} = 0.24$, $\beta = 0.04 \pm 0.10$, $P = 0.62$) and incubation attentiveness (LMM: $F_{1,56} = 0.98$, $\beta = 0.05 \pm 0.05$, $P = 0.33$). Significant and nonsignificant results for models predicting NDC production, nest guarding and incubation behaviour are summarized in Table 2.

DISCUSSION

Our results are consistent with the hypothesis that NDCs given by female song sparrows function to recruit male vigilance during incubation off-bouts. Females called more often when the male was present before nest departure, and males were also more likely to nest guard (or at least be present near the nest and actively singing) when the female gave the call. The increase in calling rate in the presence of the male does not necessarily refute the alternative hypothesis that calls act to decrease male harassment of the female (Beletsky & Orians, 1985; Edwards, 1987; McDonald & Greenberg, 1991). Indeed, in red-winged, *Agelaius phoeniceus*, and yellow-headed, *Xanthocephalus xanthocephalus*, blackbirds, males chase females that leave the nest silently significantly more often than they do females that vocalize upon nest departure. Thus, calls in these species may function to decrease harassment, which might otherwise distract females from adaptive incubation behaviour (Beletsky & Orians, 1985; Edwards, 1987). Since we have no data on chasing behaviour in song sparrows, we cannot discount the possibility that silent departures result in harassment. However, our results do suggest that NDCs do not function to increase male mate-guarding behaviour (Fedy & Martin, 2009). Specifically, males usually remained in the vicinity of the nest during the incubation off-bout following an NDC, rather than following the female, which usually left the vicinity to forage.

In addition to helping to elucidate the function of NDC behaviour, our results also grant insight into observed increases in male singing rates during the incubation stage (observed in song

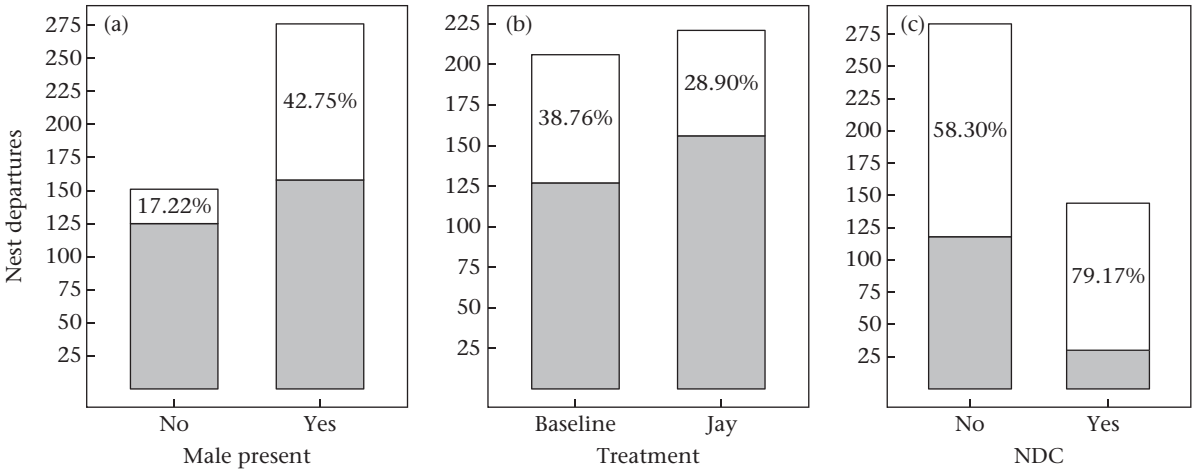

Figure 2. Percentage of nest departures during which female song sparrows produced (open bars) and did not produce (grey bars) nest departure calls (NDCs) relative to (a) the presence or absence of their mate and (b) their perceived risk of nest predation from corvids (baseline vs jay). (c) Percentage of nest departures during which males performed (open bars) and did not perform (grey bars) nest-guarding behaviour when their mates produced or did not produce NDCs.

sparrows by Foote & Barber, 2009), by suggesting that one function of male singing may be to signal his presence to the female and facilitate coordination of nest vigilance behaviour. Male singing during incubation on-bouts may serve as an 'all clear' signal to the female (Wickler, 1985: 'watchman's song' hypothesis; Lima, 2009), who may then be more likely to depart from the nest and to produce a nest departure call. Indeed, studies on house wren, *Troglodytes aedon* (Johnson & Kermott, 1991), reed buntings, *Emberiza schoeniclus* (Wingelmaier, Winkler, & Nemeth, 2007), and great tits, *Parus major* (Lind, Dabelsteen, & McGregor, 1996), all indicate that females are more likely to terminate incubation and depart the nest when the male is singing nearby, which also suggests that male song may act as a signal that no danger to the nest is imminent (Lima, 2009). Furthermore, male song during incubation off-bouts may serve as a signal to foraging females that the male is present and guarding the nest. The male could then commence to signal in a different fashion (perhaps via alarm calling) if the nest were detected and threatened.

Given that NDCs function as signals to enhance male nest guarding, calling behaviour may evolve in populations or species in which nest guarding by males is especially important to fitness. In populations with high rates of nest predation, producing NDCs to promote male nest guarding may have high fitness benefits. On the other hand, given characteristics of the NDC that make the vocalizer easy to locate, producing the call may attract predators (McDonald & Greenberg, 1991). Thus, females may elevate fitness by plastically adjusting calling behaviour to target the intended receiver (the male), while avoiding eavesdropping by predators (Zuk et al., 1995). Indeed, calling rate declined when we experimentally elevated perceived nest predation risk. Like other avian nest predators, scrub-jays have highly developed auditory systems and may cue in to NDCs when depredating nests (Eggers et al., 2006; Martin, 1987a; Peluc et al., 2008). Significantly, when not producing an NDC, females often departed from the nest silently and commenced alarm calling once off the nest (M. L. Grunst, A. S. Grunst, & J. T. Rotenberry, personal observations). In contrast to NDCs, acoustical characteristics of alarm calls, including high frequency and short duration, make localization difficult (Caro, 2005; Klump & Shalter, 2010). Thus, switching from the NDC to the alarm call in the context of high nest predation risk could provide a mechanism of alerting the male to nest departure while reducing the probability of nest detection.

In addition to predator presence, differences in the dominant predator type might also affect the adaptive advantage of producing NDCs. In contrast to avian predators, other predator guilds such as snakes have poor hearing, are unlikely to use calls to locate nests and may selectively depredate lower nests as opposed to higher ones (Martin, 1987a; Peluc et al., 2008). Furthermore, some types of predators are easier to defend against, such that intensity and efficacy of nest defence may vary with predator type (Curio, 1975; Kruuk, 1964; Patterson, Petrinovicha, & James, 1980; Winkler, 1992). If a predator is easily deterred, benefits of attracting the male might outweigh costs. Thus, an intriguing possibility is that females may actually increase calling rate when faced with predation threat from a different type of predator. We do not know the relative contribution of predator guilds to nest depredation events in our population. However, recent research on the predator community of open-cup nests in eastern Sierra riparian habitat concluded that one or a few predator species do not predominate

Table 2
Summary of main effects for nest departure call frequency of female song sparrows and male guarding behaviour and incubation attentiveness/off-bout length

Dependent variable	Independent variable	Direction of effect	*P*
Nest departure call behaviour	Male presence	+	<0.001
	Nest predator presence	−	0.01
	Male body mass	+	0.01
	Repertoire size/syllable diversity	0	0.62/0.53
	Nest elevation	0	0.72
	Time	−	0.005
	Date	0	0.90
Male guarding behaviour	Nest departure call given	+	<0.001
	Nest predator presence	0	0.42
	Male body mass	0	0.60
	Repertoire size/syllable diversity	0	0.31/0.35
	Nest elevation	0	0.64
	Time	0	0.64
	Date	0	0.99
Incubation attentiveness; off-bout length	Nest departure call given	0/trend +	0.83; 0.07
	Nest predator presence	0	0.35; 0.61
	Male body mass	0	0.16; 0.19
	Repertoire size/syllable diversity	0	0.49/0.60; 0.96/0.17
	Nest height	trend −/−	0.08; 0.05
	Time	0	0.15; 0.12
	Date	0	0.10; 0.82

(Latif et al., 2012). Therefore, females may need to assess a complex predator community when adjusting calling behaviour.

Females may also need to assess their mate's willingness or ability to nest-guard when determining whether to call. Indeed, females were more likely to give an NDC if their mate was heavier. More massive males may be in better body condition and may also be larger, and may thus be more willing or able to defend nests against predators, such that costs of attracting predators decline. Indeed, we found that females mated to heavier males took longer off-bouts than other females in the presence of the predator, but not under baseline conditions, suggesting that heavier males may be better able to protect the nest, ameliorating costs of longer off-bouts for females. Alternatively, heavier males may have higher energetic reserves that allow them to sing at higher rates, and may consequently be more likely to signal their presence near the nest to females. Studies in a number of bird species have reported a positive correlation between nest-guarding intensity and body condition (Martin & Horn, 1993; Sproat & Ritchison, 1993; Wallin, 1987; Winkler, 1992). In *M. melodia*, Rastogi, Zanette, and Clinchy (2006) demonstrated that food-supplemented birds have more time available for nest guarding and nest attentiveness than unsupplemented controls. Guarding, as measured by male presence during incubation off-bouts, was uncorrelated with male body mass in our study, suggesting that male willingness to defend the nest did not play a dominant role. However, we did not directly measure the intensity of male nest guarding, the tendency for males to take risks to defend the nest, or efficacy of deterring predators.

In contrast to body mass, NDC rate was unrelated to male song complexity, suggesting that song may convey little information regarding direct benefits provided by males via nest guarding. Male nest guarding was similarly unrelated to song complexity, corroborating this view. Interestingly, past studies on song sparrows have reported that males with more complex song repertoires are in superior body condition (Pfaff et al., 2007; Reid, Arcese, Cassidy, Hiebert, et al., 2005; Reid, Arcese, Cassidy, Marr, et al., 2005; Reid, Arcese, & Keller, 2003). Given positive correlations between multiple metrics of male quality one might expect similar correlations to arise between NDC production and different male quality metrics. However, in contrast to past work on the song sparrow, body mass and song complexity were uncorrelated in our population of breeding males. Thus, nest departure calling behaviour of females may be influenced by direct benefits associated with male body mass independent of song complexity, which may communicate indirect benefits.

In addition, females may also adjust calling behaviour based on differences in nest placement that affect vulnerability to detection by predators. We hypothesized that off-ground nests would be more vulnerable to predation by corvids (Eggers et al., 2006; Martin, 1987a; Peluc et al., 2008), such that females with elevated nests would reduce calling rate more when confronted with a predator. In support of this hypothesis, orange-crowned warblers, *Vermivora celata*, nesting in shrubs decrease offspring provisioning rates (another conspicuous parental behaviour) more in response to the presence of an avian predator than do those nesting on the ground (Peluc et al., 2008). However, we unexpectedly found that females departing from elevated nests actually called more in the presence of the predator. This result may reflect the fact that our study involved production of a conspicuous auditory cue in addition to the visual cue of a nest visit. At elevated nests, predators may be able to use the visual cue of female departure to locate the nest, whereas females may be able to depart from ground nests invisibly. Thus, calling from a lower nest may add a more substantial additional cost to departure itself than calling from a more elevated nest. Given the possibility of departure without detection from a lower nest, not calling may be adaptive, despite the fact that the male may fail to recruit for nest guarding. On the other hand, departure from a higher nest without detection may be unlikely, such that it may be adaptive to call and risk predator attraction to increase the probability of promoting male vigilance. Interestingly, females with elevated nests also had longer incubation off-bouts, which could arise if these females are more tentative when returning to the nest, due to greater nest conspicuousness.

Females also called less upon nest departure as the day progressed. The dependency of calling behaviour on time may be related to temporal variation in predation risk or male propensity to respond to calls. Specifically, costs of calling may increase later in the day due to heightened predation risk by diurnal predators. Many predators including brown-headed cowbirds, are more active towards dawn (Rothstein, Verner, & Stevens, 1984), but corvid nest predation risk may be elevated later in the day (Eggers et al., 2005; Lima, 2009), which could motivate decreases in NDC production. We did not measure temporal patterns of corvid activity at our study site. However, Eggers et al. (2005) found that corvid predation of Siberian jay, *Perisoreus infaustus*, nests increased later in the day, and that jays decreased nest visit rates accordingly. The benefits of calling could also decrease later in the day if male propensity to respond to calls declines as the day progresses. However, we found no association between male nest guarding and time of day in the present study.

Finally, neither the length of individual incubation off-bouts nor overall incubation attentiveness significantly differed as a function of NDC production or with male nest guarding behaviour. We initially hypothesized that increased male vigilance and decreased costs of staying off the nest associated with producing an NDC would result in longer incubation off-bouts following call production. Similarly, we reasoned that overall nest attentiveness might be lower at nests where females called more often. Indeed, Ziolkowski, Johnson, Hannam, and Searcy (1997) found that following temporary removal of the male, female house wrens increased incubation attentiveness by 20%, suggesting that, in at least some species, interactions between the male and female affect costs of staying off the nest, and hence incubation behaviours. However, our failure to find a relationship between NDC production, male guarding and incubation behaviours suggests that the optimal length of incubation off-bouts is not strongly affected by the heightened probability of male recruitment accomplished by giving the call. Although male nest guarding may lower costs of staying off the nest by reducing the probability of clutch loss through depredation, thermoregulatory costs of remaining off the nest also exist (Conway & Martin, 2000; Martin, Auer, Bassar, Niklison, & Lloyd, 2007; Webb, 1987). Since only females incubate, the presence of the male does not affect thermoregulatory costs. Thus, despite male nest guarding, females may still optimize fitness by minimizing off-bout length to the amount of time needed to accomplish basic self-maintenance activities (Conway & Martin, 2000).

Overall, female song sparrows appear to adaptively adjust NDC production in a pattern consistent with balancing costs of attracting predators against benefits of recruiting males to guard nests. Plasticity in calling probably exists because context-appropriate communication elevates fitness, whereas contextual mistakes in the decision to communicate result in fitness declines (Tuttle & Ryan, 1981; Zuk & Kolluru, 1998; Zuk et al., 1995). Therefore, our study aids in elucidating the complexity of communication systems in biparental species, and potential fitness ramifications of communicating in inappropriate ways.

More work is needed to fully understand context dependency in NDCs and the potential costs of calling. Examining population-level differences in call production, such as those documented in

M. melodia, may help elucidate the evolution and persistence of NDCs. In addition, the unique selective pressures of urban environments provide an opportunity to explore impacts of signal interference on call production (Bermúdez-Cuamatzin, Rios-Chelen, Gil, & Garcia, 2009; Brumm, 2004). Furthermore, learning is central to the production of species-specific song (Beecher & Brenowitz, 2005; Catchpole & Slater, 2008), but the degree to which learning shapes NDC development, the propensity to produce calls in specific contexts and persistence of calling within populations is unknown. Finally, although the frequency of NDCs appears largely stereotyped, the amplitude or duration of calls produced by females may vary either as a function of fixed differences between females, or as a plastic response to dynamic conditions. Indeed, variation in the duration of NDCs and the number of distinct notes produced during each vocalization was apparent in our data set. Such variation may convey information about female quality or energetic state and may influence male guarding behaviour.

Acknowledgments

We thank D. Dawson and other employees of the Sierra Nevada Aquatic Research Laboratory for allowing use of reserve lands to conduct this research and for providing housing and laboratory space during the field season. S. J. Myers was instrumental in obtaining a bird banding subpermit to authorize components of this study. W. Saltzman and two anonymous referees provided valuable comments on earlier drafts of this manuscript. S. Grunst and R. Grunst assisted in the field and UCR undergraduate students aided in data processing. Funding was provided by Sigma Xi, the University of California Natural Reserve System (Mildred E. Mathias Grant), Valentine Eastern Sierra Reserve, the University of California, Riverside's Graduate Division and the National Science Foundation (Doctoral Dissertation Improvement Grant).

Supplementary Material

Supplementary material for this article is available, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2014.01.010.

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